ISSN 1346-7565 Acta Phytotax. Geobot. 55 (3): 181–197 (2004)

Variation of Pitcher Morphology within *Nepenthes vieillardii* Hook. f. (Nepenthaceae) in New Caledonia

KAORUKO KURATA[1], TANGUY JAFFRÉ[2] and HIROAKI SETOGUCHI[1]

[1] *Graduate School of Human and Environmental Studies, Kyoto University, Kyoto606-8501, Japan;* [2] *Research Institute for Development, BP A5, Nouméa, New Caledonia, France*

Taxonomy of *Nepenthes* has been exclusively based on pitcher morphology that well characterizes the carnivore. In order to understand the morphological diversity and to re-examine taxonomical diagnosis of the *Nepenthes* taxa in New Caledonia, the pitcher morphology was carefully studied based on 221 matured upper pitchers of 124 individuals from seven localities of the island. For this purpose, we investigated size of pitchers and of their lids, number and density of nectar glands on lids, number and density of digestive glands in pitchers and ratio of digestive zone vs. waxy zone in pitchers. These morphological features varied widely between the populations though they are mostly stable within an individual plant. Statistical analyses did not segregate any population and supported the taxonomical treatment to unite several taxa into an insular endemic, *Nepenthes vieillardii* Hook. f. in New Caledonia. The number of digestive glands and area of digestive zone in pitcher varied greatly between populations suggesting that some ecological factors do affect the morphological diversity of pitchers.

Key words: carnivorous plants, digestive glands, morphology, nectar glands, *Nepenthes*, New Caledonia, pitcher

Nepenthes, the sole genus of the family Nepenthaceae comprises about 90 species of perennial herbs distributed in Madagascar, Seychelles, northern India, Indo-China peninsula, Malesia, northern Australia and New Caledonia (Kurata 2002). These plants could expand their distribution by adjusting to soils with poor nutrients owing to an accomplished special evolution of capturing insects by an insectivorous leaf called a "pitcher". Taxa of *Nepenthes* have been mainly classified based on the characteristics of pitcher morphology. On the other hand, dimorphism of the upper funnel pitcher and the lower jarring pitcher has been well recognized even within an individual plant (e.g., Clarke 1997). Intraspecific variation of pitcher morphology also shows a wide range in its morphological diversity (e.g., MacFarlane 1908, Kurata 1976, Komiya 1994, Phillips & Lamb 1996, Clarke 1997, Jebb & Cheek 1997). Therefore, taxonomical confusions have been caused in the current classification of *Nepenthes*.

New Caledonia, a continental island that originated from Gondwana, is covered with a large serpentine area. The ultramafic soil derived from the serpentine or gabbro is well characterized by very few nutrients for plant growth and hyper-magnesium content and the *Nepenthes* plant is well adapted to the edaphic conditions. Concerning the species in New Caledonia, nine taxa including six endemic species have been described mainly based on the

morphology of the pitcher (Hooker 1873, Dubard 1906, Macfarlane 1908, Guillaumin 1911, Moore 1921, Danser 1928, Guillaumin 1953, 1964, Jebb & Cheek 1997). These taxa of *Nepenthes* in New Caledonia have been described based on small number of specimens, and it is uncertain whereabouts in the plant body the pitchers were collected.

Moreover, Jebb & Cheek (1997) integrated all taxa reported from New Caledonia, as a synonym of *Nepenthes vieillardii* Hook. f. without any explanations. Further examination of the morphological diversity among New Caledonian *Nepenthes* is needed to clarify the morphological diversity quantitatively and to verify the classification of the species.

As contribution to a critical examination of the taxonomic problems of *Nepenthes* in New Caledonia, we clarified in this study the variation of pitcher morphology in *Nepenthes vieillardii sensu lato* in New Caledonia by quantitative analyses on the size of the pitcher and its lid, the number and density of the nectar glands and digestive glands, and the ratio of the digestive zone and waxy zone in the pitcher. Classification of New Caledonian *Nepenthes* has been discussed by comparison among the collection sites. The nomenclature tentatively follows that of Jebb & Cheek (1997).

Materials and Methods

Study sites and materials

Plants of *Nepenthes vieillardii* grow in maquis vegetation (Brooks 1987) developed on ultrabasic soil originating from serpentine rock or gabbro. The plants usually develop small populations isolated from each other. *Nepenthes* in New Caledonia usually grown in sunny place like that of opened slope, riverbank or edge of the forest. The plant is creeper of several meters in length, and develops leaf-pitchers on the top of shoot while withering lower leaf-pitchers. Therefore the plants frequently have several matured upper funnel pitchers in serpentine area with poor nutrient. The populations examined in the present study were chosen from nearly entire area of distribution range of the species, moreover, five of the seven populations examined were located in the southern part of the island (Fig. 1 and Table 1-A) where the serpentine soil is widely distributed (ORSTOM 1983). Population of GR is developed on gabbro and the remainders on serpentine.

Prior to the analysis between the populations, morphological variation of pitcher within an individual was examined. Plants of *Nepenthes vieillardii* usually have several matured pitchers and we could collect many pitchers, enough for statistical analysis at CP, GR, MK among the seven populations and additional RA and BL (Table 1-B). 14 - 28 pitchers were sampled from each individual in the five collection sites.

For analysis on the inter-populational variation of pitcher morphology, we collected a matured upper pitcher from each individual, and eight to 28 matured pitchers were sampled from each locality. In total, 119 pitchers were used for the measurements (Table 1-A). Since removal of pitchers was expected to seriously damage the individual, pitchers were collected from large individuals with many pitchers. The collected pitchers were fixed with FAA (50% ethanol: acetic acid: formalin = 90: 5:5).

Measurements

Seven morphological characters were measured (Fig. 2): size of lid (maximum and minimum diameter of lid), length and width of pitcher and height of digestive gland zone were measured using a scale; the number and density of nectar glands on the lid and digestive glands in the pitcher were counted under a stereoscopic microscope (Olympus SZ4045, Olympus Co., Ltd.). We did not use characteristics such as color, shape and presence or absence of the fringe for this analysis because the pitchers showed large variations even within one plant (Fig.

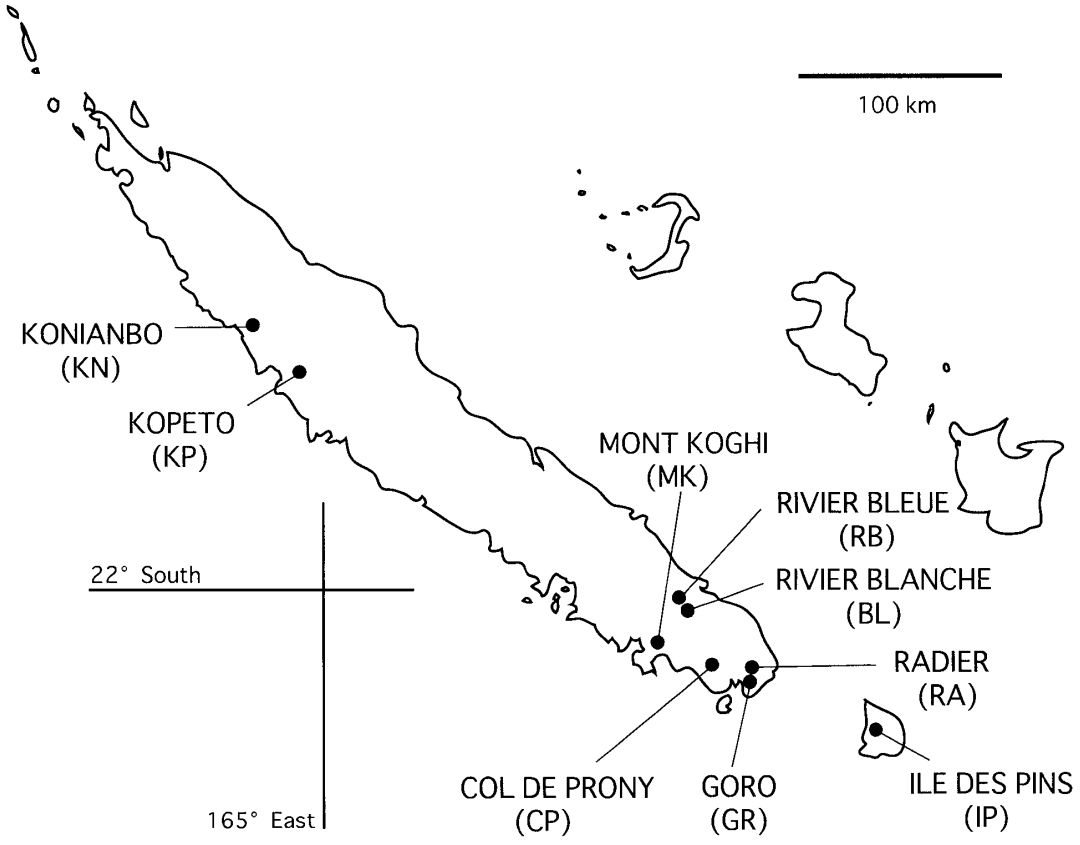


FIG. 1. Map showing the locations of nine collection sites of *Nepenthes vieillardii* in New Caledonia.

TABLE 1. Collection sites and samples of *Nepenthes* in New Caledonia.

A. Inter-populational variation of pitcher morphology.

Code for study site	Locality	Altitude (m)	Soil type	Number of pitchers examined	Habitat
IP	Ile des Pins	30	Serpentine	10	Wet riverbank
GR	Goro	80	Gabbro	28	Open slope
CP	Col de Prony	320	Serpentine	15	Open slope
MK	Mont Koghi	420	Serpentine	28	Shrub
RB	Riviere Bleue	220	Serpentine	21	Edge of the forest
KN	Koniambo	830	Serpentine	9	Open slope
KP	Kopeto	810	Serpentine	8	Edge of the forest

B. Variation of pitcher morphology within one plant.

Sample No.	Locality	Code for study site	Soil type	Number of pitchers examined	Habitat
1	Mont Koghi	MK	Serpentine	28	Shrub
2	Riviere Blanche	BL	Serpentine	14	Open slope
3	Goro	GR	Gabbro	15	Open slope
4	Col de Prony	CP	Serpentine	25	Open slope
5	Radier	RA	Serpentine	20	Open slope

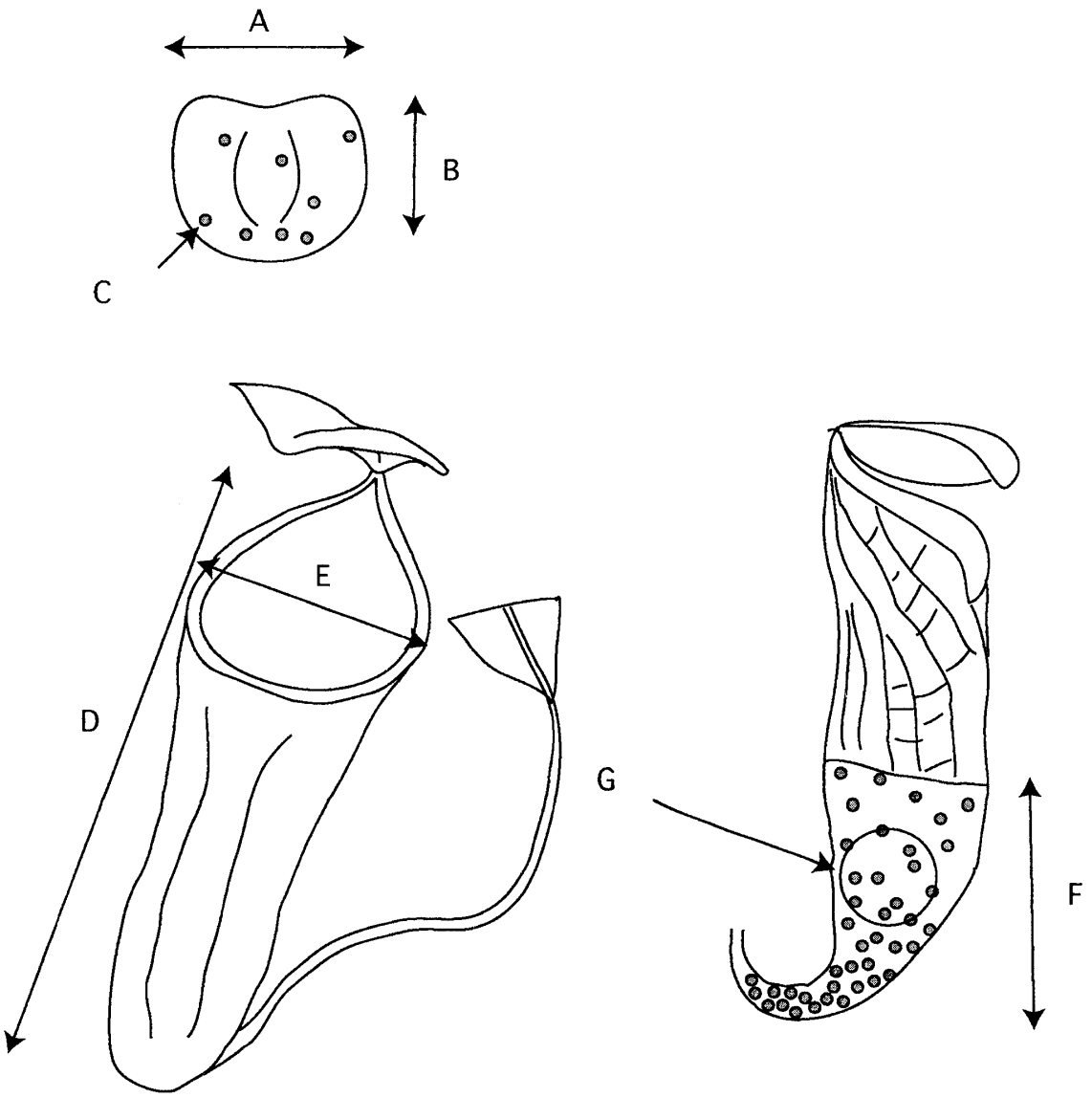


FIG. 2. Measurement of pitchers and lids of *Nepenthes vieillardii*. A. Length of maximum diameter of lid. B. Length of minimum diameter of lid. C. Total number of nectar glands. D. Length of pitcher. E. Width at the widest part of pitcher. F. Height of digestive gland zone of pitcher. G.. Number of digestive glands per unit area.

3). The area of the lids was calculated from the maximum and minimum diameter, and the density of the nectar glands was estimated. The density of digestive glands per square was calculated from the area of the leaf piece cut-off by the leaf punch.

Specimens of *Nepenthes vieillardii*, *N. vieillardii* var. *deplanchei* Dubard, *N. vieillardii* var. *montrouzierii* Dubard and *N. vieillardii* var. *minima* Guillaumin including their type specimens were examined for measurement of their pitcher morphology. The available specimens were the four of the nine taxa described from New Caledonia. 26 pitchers from 12 sheets of *N. vieillardii*, 15 pitchers from six sheets of *N. vieillardii* var. *deplanchei*, five pitchers from one sheet of *N. vieillardii* var. *minima* and 13 pitchers from three sheets of *N. vieil-*

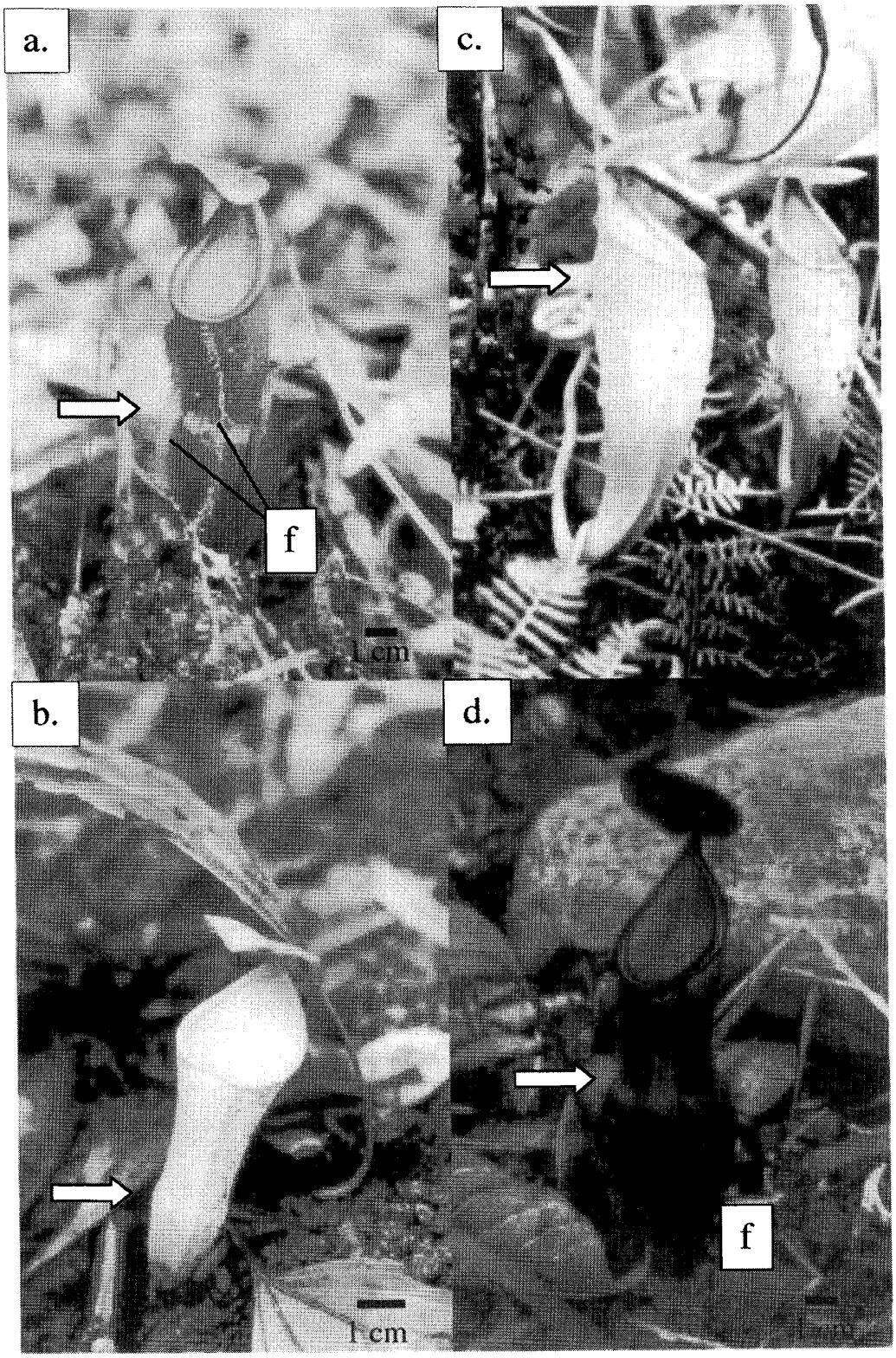


FIG. 3. Gross morphology of pitchers of *Nepenthes vieillardii*. The color and the shape of the pitcher varied among plants. The arrows indicate the boundary between the digestive gland zone and waxy zone. a, b and d were from RB, and c was from MK. f: indicate fringe.

lardii var. *montrouzierii* were examined for the morphology. List of specimens examined were listed in appendix.

Statistical analysis

Statistical analyses were performed using the mean value for the characters of each individual. The data were subjected to analysis of variance (one-way ANOVA) with the Tukey's honestly significant difference test (Tukey's HSD) using SPSS ver. 10.0 J for Windows (SPSS 2000).

Results

Variation of pitcher morphology within one individual and between individuals

The seven morphological characters were measured for 102 pitchers from five individuals, and the mean value and standard error of the measurement of each plant were presented in Table 2-A. The standard errors for each measurement in individual were lower than the value among the individual (Fig. 4). The mean value is remarkably different from each individual. Nectar gland density ranged from 6.6 (sample 4) to 24.3 nos./cm^2 (sample 1) and was remarkably high in sample 1 among the five individuals. On the other hand, ratio of digestive gland zone / length of pitcher was 0.59 in sample 2, indicating the highest value among the five individuals examined (Fig. 5). The significant difference was detected between all individual plants excluding the density of the digestive gland ($p < 0.01$, Tukey's HSD, Table 3-B).

Inter-populational variation

1) Size of lid and pitcher

The variation of the area of lids is shown in Table 2-B. The area of lids in KP was significantly different from that in other populations. The mean value is larger (mean 14.4 cm^2) than twice of those in GR, CP and MK (mean 5.6 - 6.6 cm^2).

Variations in the size of the pitcher are also given in Table 2-B. Length and width of pitcher on plants from KP are larger than these from other localities (mean 13.5 cm in length and 4.4 cm in width in KP). On the other hand, pitcher in plants from GR, MK and KN were relatively smaller; width of the GR specimens (2.3 cm) was almost half of specimens from KP.

2) Nectar glands

Number of nectar glands on the lid of plants from KP was markedly higher than those from other localities (145.1 glands on lid); less than one-third of glands were distributed on the lid of specimens from GR (Table 2-B).

The area of the lid was calculated from the lengths of the maximum and minimum diameters, and the density of the nectar gland on the lid at each collection site was also estimated. Intrapopulational variation and comparison among the populations in the density of the nectar gland on the lid are presented in Fig. 6. The value showed a variation range of 17.4 (KN) - 7.7 n./cm^2 (RB), indicating great variability.

The relation between the area of the lid and the number of nectar glands is given in Fig. 7. A correlation was recognized between these two factors (Correlation coefficient = 0.5271, $p < 0.001$). The number of nectar glands was changed in proportion to the area of the lid. However, the density of the nectar glands is an unstable character on account of the large variation within a population.

The distribution of nectar glands is shown in Fig. 8-a. The nectar glands of *Nepenthes vieillardii* were sparsely distributed throughout the entire lid.

3) Digestive glands

The density of the digestive glands, the total number of digestive glands and the ratio of the digestive gland zone are also shown in Table 2-B.

The variation range in the density of digestive glands on a pitcher was 442.0 glands per cm^2 in IP to 733.7 glands in GR (Fig. 9). No significant dif-

TABLE 2. Mean and standard error of morphological characters of pitchers collected at each locality.

A. Variation of pitcher morphology within one plant.

Sample No.	Area of lid (cm^2)	Total number of nectar glands (n.)	Density of nectar glands (n./cm^2)	Length of pitcher (cm)	Width of pitcher (cm)	Density of digestive glands (n./cm^2)	Total number of digestive glands (n.)	Ratio of digestive zone
1	3.2 ± 0.15	74.6 ± 2.45	24.3 ± 1.21	6.0 ± 0.12	1.9 ± 0.04	789.4 ± 46.41	12081.6 ± 279.03	0.45 ± 0.01
2	3.5 ± 0.26	36.4 ± 2.54	10.8 ± 0.70	6.8 ± 0.28	2.0 ± 0.08	617.3 ± 50.21	14356.2 ± 486.69	0.59 ± 0.03
3	3.6 ± 0.37	50.7 ± 5.50	14.3 ± 0.88	7.8 ± 0.39	1.9 ± 0.11	491.3 ± 27.57	8576.6 ± 406.24	0.40 ± 0.01
4	7.0 ± 0.39	45.1 ± 2.14	6.6 ± 0.29	10.1 ± 0.26	2.5 ± 0.08	692.5 ± 29.19	21099.3 ± 537.00	0.40 ± 0.00
5	4.6 ± 0.31	43.3 ± 2.56	9.7 ± 0.40	9.1 ± 0.25	2.4 ± 0.07	736.0 ± 45.28	22785.5 ± 417.61	0.48 ± 0.01

B. Inter-populational variation of pitcher morphology.

Collection site	Area of lid (cm^2)	Total number of nectar glands (n.)	Density of nectar glands (n./cm^2)	Length of pitcher (cm)	Width of pitcher (cm)	Density of digestive glands (n./cm^2)	Total number of digestive glands (n.)	Ratio of digestive zone
IP	7.3 ± 1.13	55.0 ± 8.91	7.8 ± 0.70	11.1 ± 0.85	3.0 ± 0.27	442.0 ± 29.95	22861.7 ± 3122.24	0.47 ± 0.02
GR	5.6 ± 0.41	48.6 ± 3.24	9.2 ± 0.99	9.3 ± 0.42	2.3 ± 0.10	733.7 ± 45.14	19624.2 ± 310.73	0.43 ± 0.01
CP	6.6 ± 0.81	89.9 ± 11.07	11.4 ± 2.09	10.5 ± 0.51	2.5 ± 0.13	611.3 ± 61.56	17054.1 ± 589.36	0.37 ± 0.02
MK	6.2 ± 0.43	93.4 ± 12.04	14.9 ± 1.35	9.3 ± 0.20	2.7 ± 0.05	504.1 ± 42.23	16398.6 ± 516.34	0.46 ± 0.02
RB	9.0 ± 0.76	65.2 ± 6.32	7.7 ± 0.78	12.6 ± 0.94	3.3 ± 0.18	580.9 ± 41.60	28798.1 ± 1971.72	0.43 ± 0.02
KN	7.8 ± 1.97	95.6 ± 6.63	17.4 ± 2.82	8.5 ± 0.93	2.9 ± 0.31	689.1 ± 92.59	19843.4 ± 1935.09	0.43 ± 0.03
KP	14.4 ± 1.92	145.1 ± 16.05	10.8 ± 1.35	13.5 ± 1.14	4.4 ± 0.35	590.0 ± 79.66	40231.1 ± 3437.46	0.38 ± 0.03

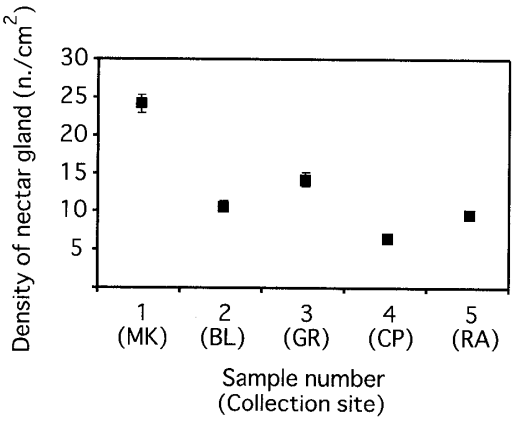


FIG. 4. Mean and standard error of density of nectar glands collected from five individual plants.

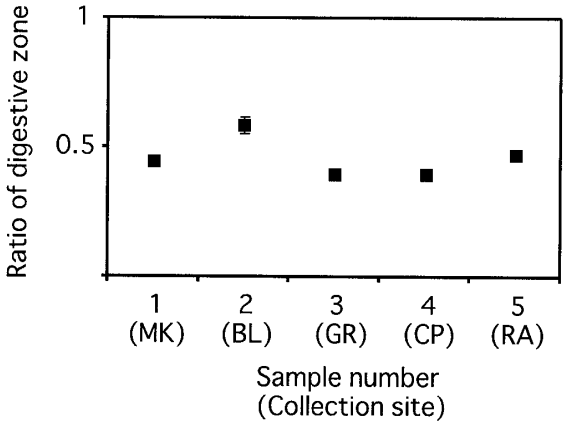


FIG. 5. Mean and standard error of ratio of digestive gland zone collected from five individual plants.

TABLE 3. Significant difference of morphological characters in one plant using Tukey's HSD test . (*p<0.05, **p<0.01)

A. Density of nectar gland

Sample No.	1	2	3	4	5
1	-				
2	0.000**	-			
3	0.000**	0.111	-		
4	0.000**	0.016*	0.000**	-	
5	0.000**	0.945	0.008**	0.064	-

B. Density of digestive gland

Sample No.	1	2	3	4	5
1	-				
2	0.054	-			
3	0.000**	0.395	-		
4	0.355	0.762	0.015*	-	
5	0.875	0.389	0.003**	0.942	-

C. Total number of digestive gland

Sample No.	1	2	3	4	5
1	-				
2	0.006**	-			
3	0.000**	0.000**	-		
4	0.000**	0.000**	0.000**	-	
5	0.000**	0.000**	0.000**	0.041*	-

D. Ratio of digestive zone

Sample No.	1	2	3	4	5
1	-				
2	0.000**	-			
3	0.074	0.000**	-		
4	0.012*	0.000**	1.000	-	
5	0.435	0.000**	0.002**	0.000**	-

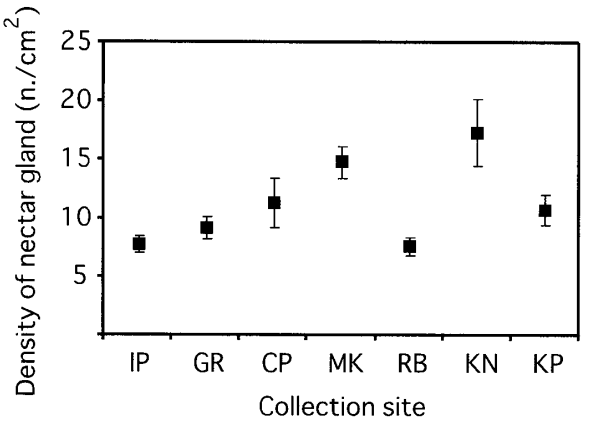


FIG. 6. Mean and standard error of density of nectar glands collected at seven localities.

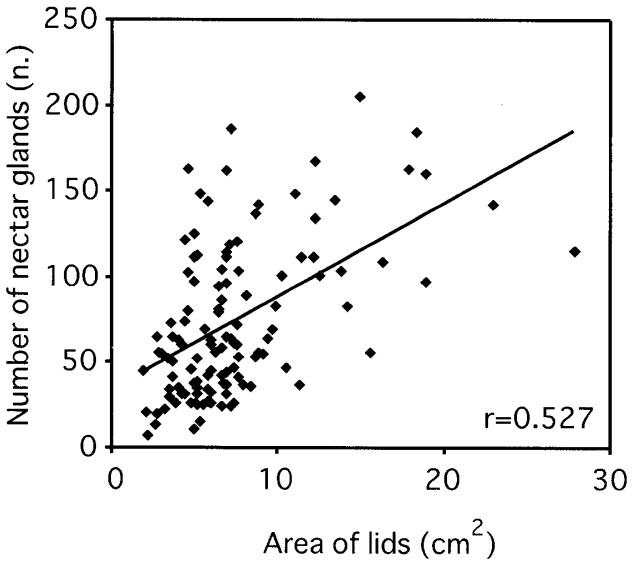


FIG. 7. Diagram showing correlation between the area of lids and the number of nectar glands of the pitcher at each locality. Correlation index = 0.5271.

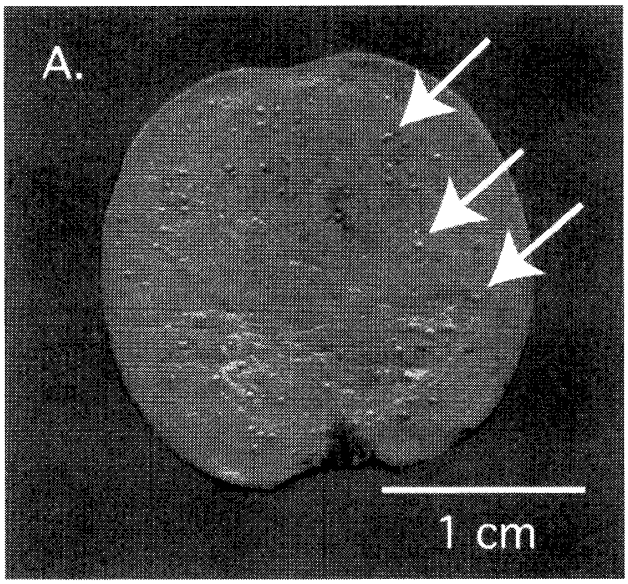
ference was recognized in the density of the digestive glands detected at each collection site, however, significant differences were found between in IP and GR, GR and MK (Tukey' HSD, $p < 0.01$, Table 4-B). To examine the relation between the size of the pitcher and the density of the digestive gland, the correlation between length and the maximum width of the pitcher was examined (Fig. 10). A relatively strong correlation was recognized between length and the maximum width of a pitcher (Correlation coefficient = 0.7446, $p < 0.001$). Therefore we used length of pitcher for representing the size of pitcher in further study. On the other hand, correlation was not recognized between the size of the pitcher and the density of digestive glands (Correlation coefficient = -0.214, $p < 0.05$, Fig. 11).

The shape of the pitcher was assumed to be a column for estimating the total number of digestive glands in a pitcher based on the maximum width of the pitcher, the height of the digestive gland zone and the density of the digestive gland. The total number of digestive glands on the pitcher of plants from KP was significantly higher than those from other localities (mean 40,231.1 glands on pitcher); more than twice of those at IP, GR, CP, MK and KN (mean 16,398.6 - 22,861.7 glands/cm^2) as shown in Table 2-B. The variation and comparison among populations in the number of digestive glands on the pitcher are presented in Fig. 12. The total number of digestive glands showed a relatively strong correlation with the area of the digestive zone (correlation coefficient = 0.7763, $p < 0.001$, Fig. 13).

On the other hand, no significant difference was observed in the ratio of the digestive gland zone (digestive zone/total length of pitcher) among the collection sites except at CP and MK (Fig. 14, Table 4-D). The maximum mean value was 0.47 at IP, and the minimum was 0.37 at CP. The mean value of the ratio of the digestive gland zone was 0.5 or less in all the sites, it was clarified as characteristics of *Nepenthes vieillardii* that the digestive gland zone was distributed below the lower half of the length of the pitcher. However, the distribution (depth) of the digestive gland zone varied among each pitcher (Fig. 8-b).

Measurement of Herbarium specimen

59 pitchers from four taxa of New Caledonian *Nepenthes* were examined based on the herbarium specimens including their types. Average and stan-



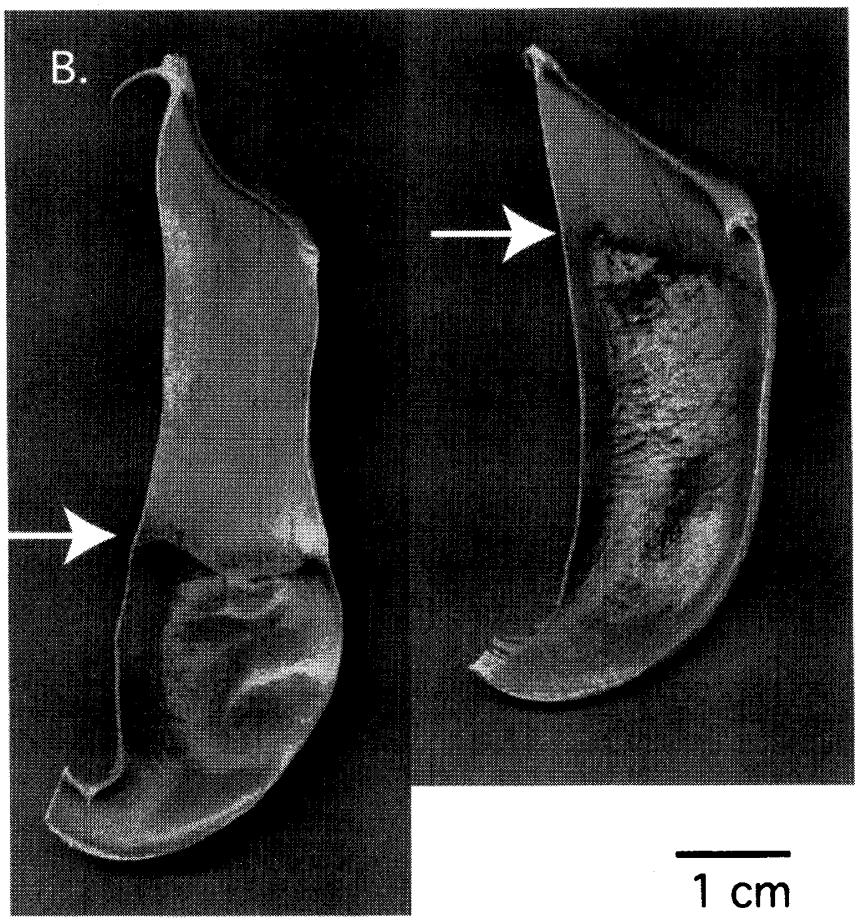


FIG. 8. Distribution of nectar glands on lids collected at KP. The nectar glands of *Nepenthes vieillardii* were sparsely distributed throughout the entire lid. b. Longitudinal sections of pitchers in KP. The distribution of the digestive gland zone was variable in each pitcher. The arrow shows the boundary between the digestive gland zone and the waxy zone.

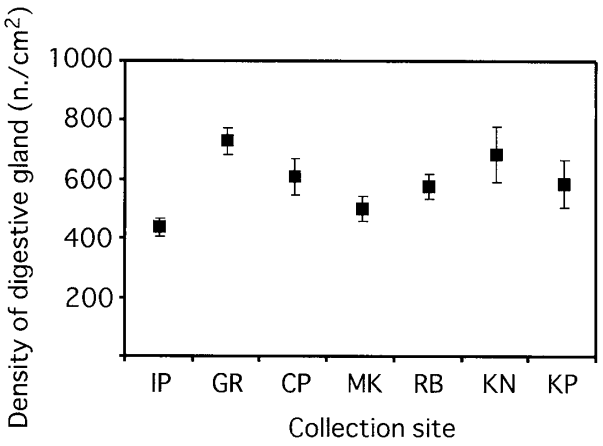


FIG. 9. Mean and standard error of density of digestive ground at seven localities.

TABLE 4. Significant difference of morphological characters using Tukey's HSD test in each locality. *p<0.05, **p<0.01

A. Density of nectar gland

site	IP	GR	CP	MK	RB	KN	KP
IP	-						
GR	0.995	-					
CO	0.763	0.920	-				
MK	0.026*	0.010*	0.518	-			
RB	1.000	0.972	0.530	0.001**	-		
KN	0.011*	0.009**	0.206	0.926	0.002**	-	
KP	0.939	0.995	1.000	0.605	0.870	0.259	-

B. Density of digestive gland

site	IP	GR	CP	MK	RB	KN	KP
IP	-						
GR	0.007**	-					
CO	0.470	0.568	-				
MK	0.986	0.002**	0.712	-			
RB	0.633	0.186	1.000	0.880	-		
KN	0.171	0.998	0.978	0.283	0.869	-	
KP	0.775	0.642	1.000	0.954	1.000	0.964	-

C. Total number of digestive gland

site	IP	GR	CP	MK	RB	KN	KP
IP	-						
GR	0.660	-					
CO	0.165	0.783	-				
MK	0.051	0.329	1.000	-			
RB	0.322	0.000**	0.000**	0.000**	-		
KN	0.853	1.000	0.900	0.680	0.002**	-	
KP	0.000**	0.000**	0.000**	0.000**	0.000**	0.000**	-

TABLE 4. continued

D. Ratio of digestive zone

site	IP	GR	CP	MK	RB	KN	KP
IP	-						
GR	0.903	-					
CO	0.055	0.192	-				
MK	1.000	0.774	0.007**	-			
RB	0.877	1.000	0.316	0.747	-		
KN	0.916	1.000	0.658	0.875	1	-	
KP	0.285	0.702	1.000	0.157	0.797	0.924	-

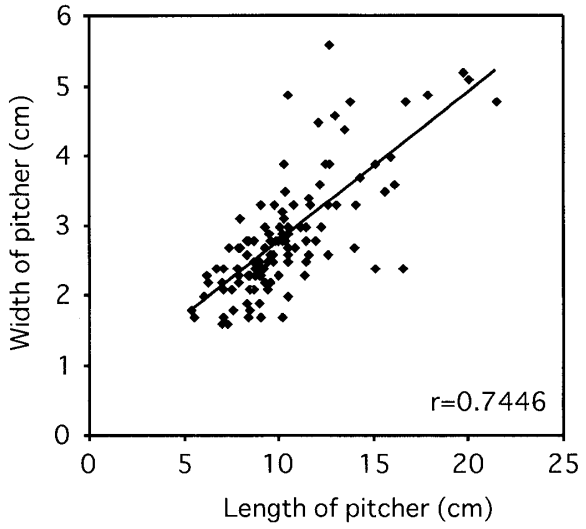


FIG. 10. Diagram showing correlation between the length and the width of pitchers collected at all localities. Correlation index = 0.7446.

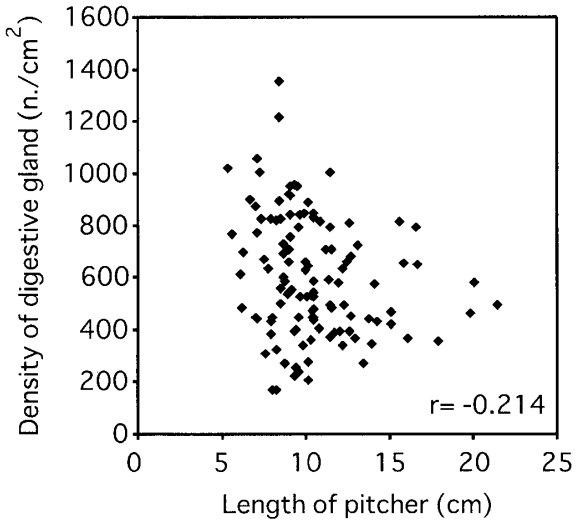


FIG. 11. Diagram showing correlation between the length of the pitcher and the number of digestive glands collected at each locality. Correlation index = -0.214.

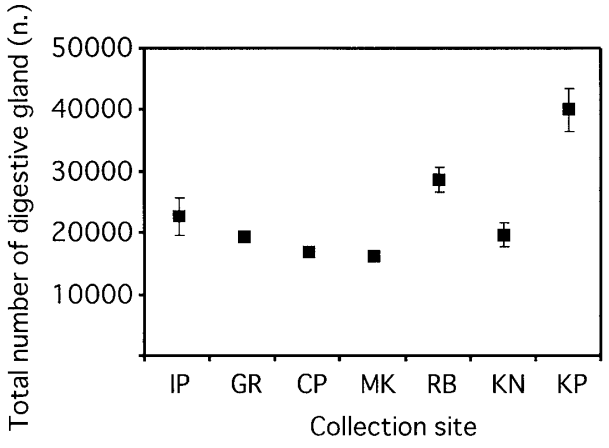


FIG. 12. Mean and standard error of total number of digestive glands at seven localities.

dard error of pitcher length were calculated in *N. vieillardii*, *N. vieillardii* var. *deplanchei*, *N. vieillardii* var. *minima* and *N. vieillardii* var. *montrouzierii* (Table 5). *N. vieillardii* and *N. vieillardii* var. *deplanchei* showed almost same value of pitcher length and width (length of 9.28-10.03 cm, width of 1.67-1.75 cm). The length of pitcher of *N. vieillardii* var. *montrouzierii* was about half of these two taxa (length of 4.63 cm, width of 0.95 cm), and size of *N. vieillardii* var. *minima* was especially smaller than that of the remainders (length of 1.12 cm, width of 0.30 cm). The pitcher size data measured in the

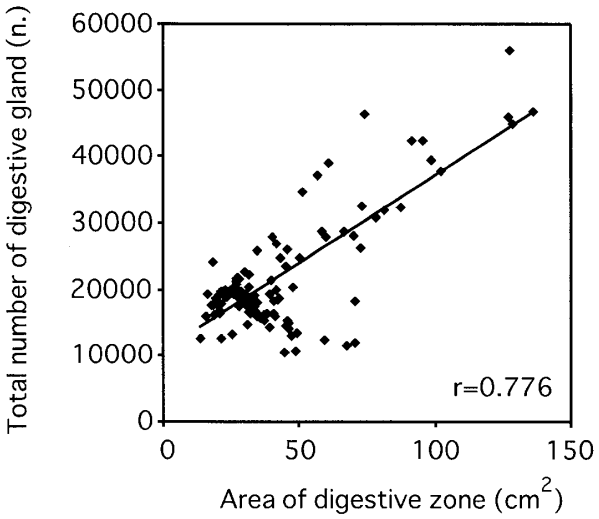


FIG. 13. Diagram showing correlation between the area of the digestive gland zone and the total number of digestive glands collected at all localities. Correlation index = 0.7763.

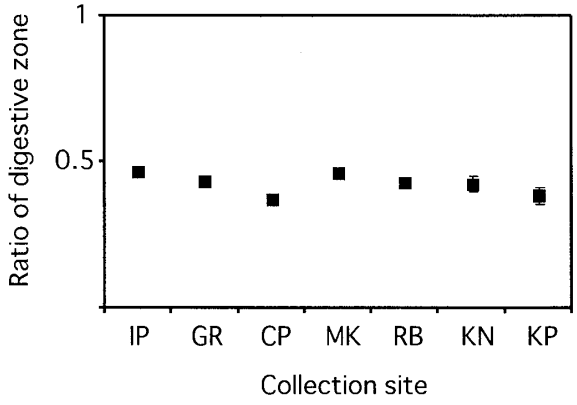


FIG. 14. Mean and standard error of the ratio of the digestive zone collected at seven localities. The mean values of the ratio of the digestive gland zone are 0.5 or less in all sites.

TABLE 5. Length and width of pitchers of herbarium specimens and the original description in each taxa of *Nepenthes vieillardii*.

	N. vieillardii	*N.vieillardii* var. *deplanchei*	*N.vieillardii* var. *minima*	*N.vieillardii* var. *montrouzierii*
Length				
in description	5.0-15.5	-	0.9-1.4	5.0-15.5
Max / Min in type specimen	12.0 / 10.0	16.5 / 8.0	1.7 / 0.7	8.0 / 6.0
Max / Min in specimens	15.5 / 3.5	16.5 / 6.0	1.7 / 0.7	8.0 / 2.7
Mean ± SE in specimens	9.28 ± 0.68	10.03 ± 0.90	1.12 ± 0.17	4.63 ± 0.46
Width				
in description	-	-	-	-
Max / Min in type specimen	2.0 / 1.0	2.2 / 1.0	0.4 / 0.2	1.3
Max / Min in specimens	3.2 / 0.9	2.3 / 1.6	0.4 / 0.2	1.4 / 0.5
Mean ± SE in specimens	1.75 ± 0.13	1.67 ± 0.11	0.30 ± 0.04	0.95 ± 0.10
Number of pitchers examined	26	15	5	13

herbarium specimen was compared with the pitcher size obtained from seven populations (Fig. 15). No pitcher was included in the ranges of pitcher size of *N. vieillardii* var. *montrouzierii* and *N. vieillardii* var. *minima*. 74.8% of the pitchers measured from the seven populations in this study were included within the range of *N. vieillardii*. Pitcher size of all populations except KP was included in the variation range of *N. vieillardii*. Especially all pitchers of CP were included within this range. 23.5% of the pitchers measured in the present study were excluded from any variation range of four varieties of *N. vieillardii*, *N. vieillardii* var. *deplanchei*, *N. vieillardii* var. *montrouzierii* and *N. vieillardii* var. *minima* based on the definition by their type specimens and taxonomic diagnosis. The excluded pitchers were collected from six of the seven populations (GR, IP, KN, KP, MK and RB), particularly, all pitchers collected from KP were not included in any variation range of the four varieties of *N. vieillardii*. However,

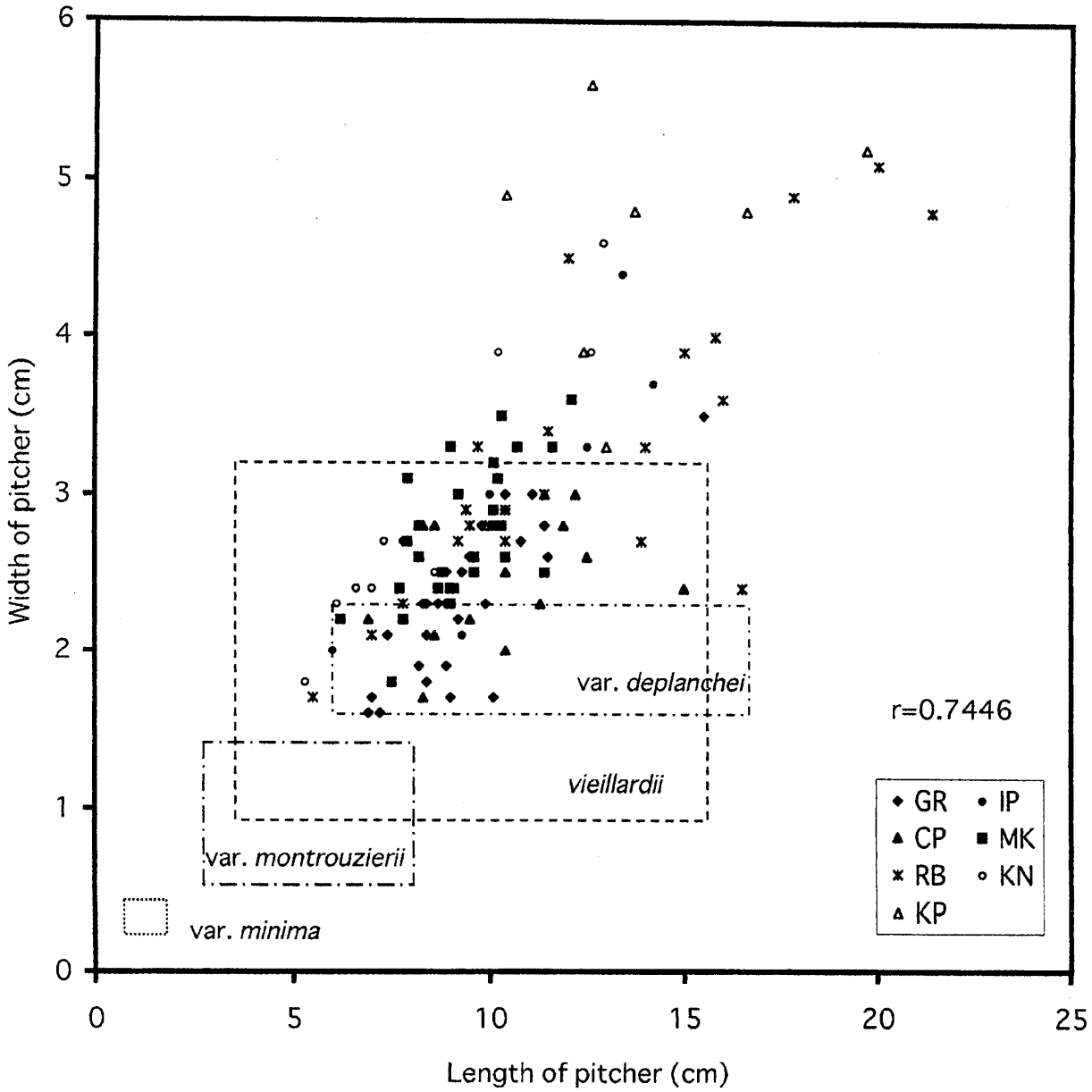


FIG. 15. Diagram showing correlation between the length and the width of pitchers collected at each locality and ranges of the pitcher size (maximum and minimum value) in three taxa of herbarium specimen. Correlation index = 0.7446.

size of pitchers varied continuously among the populations and pitchers.

Discussion

Plants of *Nepenthes* depend on the carnivorous leaf structure for the nutrient uptakes, and the pitcher structure plays an important role for their survival. Therefore pitcher morphologies representing pitcher length and width, area of lids, number of nectary on lid and number and density of digestive glands should involve their ecological role in adaptation to their habitat. Therefore we expected wide variation range in the pitcher morphology between populations which attributed to their ecological adaptation to their microhabitat even within a sole species. However, morphological variation of the pitcher has never been considered for the taxonomy in the genus *Nepenthes*. Species from New Caledonia have been also recorded on the basis of the typo-

logical pitcher morphology on a few or single individuals. This paper is the first report to examine the variation of pitcher morphology in a species of *Nepenthes*.

Morphological differentiation

The range of variation was very small in the all measured morphologies within an individual (Table 2-A). The results of the present study clearly indicated that pitcher morphology of *Nepenthes* is stable within an individual while it differs significantly between populations in New Caledonia (Table 3). The measured characteristics are almost stable in each local population, and applicable comparing pitcher morphology between populations (Table 2-B).

The results of the present study clearly indicated that New Caledonian *Nepenthes* shows little variation within an individual while exhibiting wide range of variation between populations. Even when a significant difference was not observed among all collection sites, the pitcher morphology is significantly different in maximum and minimum value habitats. For example, pitchers from KP and other localities mutually showed significant differences in the total number of digestive glands ($p < 0.01$, Tukey's HSD test, Fig. 12 and Table 2-B). The mean number of digestive glands in pitchers from KP was about twice of those from the GR, CP, MK and KN. The high number in KP pitchers is attributed to the size of the pitcher, especially to larger size in width (Table 2-B), although the density of the digestive glands and the ratio of the digestive zone were relatively low among the collection sites (Figs. 9 and 14). Total number of nectar glands on the lid was also significantly larger in KP (Table 2-B) that is also attributed to the larger size of the lids (density of nectar glands was average in KP). Therefore, *Nepenthes* plants grown in KP produce larger pitchers with many digestive glands and nectar glands, on the other hand, plants in other sites produced smaller pitchers relative to their investment for carnivory.

Ultrabasic soils originated from serpentine rock in New Caledonia contain very few nutrients, and pitcher structure is estimated to be very important for carnivory to obtain nutrients in the habitats. Therefore, pitcher structure in New Caledonian *Nepenthes* might reflect some ecologically adaptive factor and is evaluated as useless in the classification. The morphological characteristics, such as flowers, fruits and inflorescence morphologies should be investigated to support an establishment of better classification system in New Caledonia. Some ecological factors, e.g., difference in quantity and structure of prey fauna at each locality might affect the pitcher structure as an investment for carnivory. Further investigations focused on the comparative ecology between the populations are needed to clarify the pitcher polymorphisms in *Nepenthes*.

Nepenthes *Taxonomy in New Caledonia*

In the present study, we quantitatively analyzed pitcher morphology of *Nepenthes vieillardii* from the seven localities in New Caledonia. As nine taxa have been described based on the typological pitcher morphology from the island, we also confirmed the variability in the morphologies in the present analyses. All characteristics examined: size of pitchers and lids, density of nectar glands and digestive glands, total number of nectar glands and digestive glands, and the ratio of the waxy zone vs. digestive zone in pitchers showed a wide variation range among populations. The quantitative analyses could not segregate any population among the seven localities in New Caledonia although the mean values of several characteristics (e.g., total number of nectaries and digestive glands per pitcher) showed distinctive differences among several populations.

In the previous studies, intraspecific variation of pitcher morphology was recognized as larger than that found in the present study. For example, density, shape and size of nectar glands on the lid differed greatly between species in *Nepenthes* (Kurata

1976). Jebb & Cheek (1997) referred to the difference in the density, distribution and size of nectar glands on the lid between *Nepenthes vieillardii* from New Guinea and New Caledonia, and segregated the New Guinean species as *N. lamii* (e.g., 75-100 nectaries /cm^2 in *N. vieillardii* and 1,500-2,000 nectaries in *N. lamii*). Therefore, the variability of pitcher morphology in New Caledonian *Nepenthes* should be regarded as minor.

The taxonomic treatment of *Nepenthes* from New Caledonia has been controversial. Possibly due to the traditional taxonomy in the genus that has been exclusively based on the typological pitcher morphology. The length of the pitcher was widely spread with 8.5-13.5cm of mean value, and not able to be divided by each population. Pitcher size by samples at each locality was more wide-ranging than the value indicated by the specimen measurement (Fig. 15). 74.8% of the pitchers measured from the seven populations in this study were included within the range of *Nepenthes vieillardii*, however 23.5% of the pitchers measured in the present study were excluded from any variation range of the four varieties. The excluded pitchers were collected from six of the seven populations. Moreover, the size of pitcher of the herbarium specimen overlapped among *N. vieillardii*, *N. vieillardii* var. *deplanchei* and *N. vieillardii* var. *montrouzierii*. Thus, the typological taxonomy by pitcher morphology in *Nepenthes* in New Caledonia is not appropriate.

In the herbarium specimen, small variation was observed in the size of pitcher in same individual plant. *Nepenthes vieillardii* var. *minima* was described based on the small pitchers, and we confirmed that the taxonomic diagnosis is based on pitchers on juvenile rosette of the holotype specimen (Pitcher length is under 2 cm). Hooker (1873) observed that pitcher morphology of juvenile rosette is minute in size compared to upper pitchers, however, the polymorphisms of pitchers in *Nepenthes* have never been considered in the report *N. vieillardii* var. *minima* by Guillaumin (1953). Thus the taxonomic confusions in New Caledonian *Nepenthes* are attributed to the ignorance of polymorphism of pitchers. We tentatively support the taxonomic treatment by Jebb & Cheek (1997) to unit all taxa into *Nepenthes vieillardii* Hook.f. based on the pitcher morphology.

We thank Mr. Christophe Lanbert at Provinse Sud Government, Mr. Jean-Jerome Cassan at the Department of Economic Development and Environment in Province Nord, Mr. Stephan Macoy at Goro Nickel Co. and Mr. Marc-Antonie Audet at Falconbridge Co. for arranging our sampling in New Caledonia.

References

Brooks, R. R. 1987. Serpentine and its vegetation. A multidisciplinary approach. Dioscorides Press, Portland, OR.

Clarke, C. 1997. *Nepenthes* of Borneo. Kota Kinabalu: National History Publications.

Danser, B. H. 1928. The Nepenthaceae of the Netherlands Indies. Bull. Jard. Bot. Buitenzorg, Ser. 3. 10: 249-438.

Dubard, M. M. 1906. Nepenthacees de Madagascar et de la Nouvelle-Calédonie. Bull. Mus. Hist. Nat. 12: 62-67.

Guillaumin, A. 1911. Plantes phanerogames de la Nouvelle-Calédonie. Ann. Mus. Col. Mars. 2. 9: 211-212.

——. 1953. Flora de la Nouvelle-Calédonie. Mem. Mus. Nat. Hist. N. S. Ser. B. 4: 61-62.

——. 1964. Mission Franco-Suisse en Nouvelle-Calédonie. Nepenthacees. Mem. Mus. Nat. Hist. Nat. N. S. Ser. B. 15: 23-24.

Hooker, J. D. 1873. Nepenthaceae. A. D. C., Prodr. 17: 104-105.

Jebb, M., & M. Cheek. 1997. A skeletal revision of *Nepenthes* (Nepenthaceae). Blumea 42: 1-106.

Komiya, S. 1994. The Insectivorous Plants. Shokken-Jigyou, Tokyo. (In Japanese)

Kurata, Sh. 1976. *Nepenthes* of Mount Kinabalu. Sabah national parks trustees, Sabah, Malaysia.

——. 2002. Revision trial in recent enumeration of *Nepenthes* species. Proceedings of the 4th International Carnivorous Plant Conference, Tokyo, Japan.

111-116.
Macfarlane, J. M., 1908. Nepenthaceae, In: A. Engler, Das Plfanzenreich (Engler, A., ed.), 4: 1-92.
Moore, S. 1921. Plants from New Caledonia. Nepenthaceae. J. Linn. Soc., Bot. 45: 380-381.
ORSTOM. 1983. Atlas de la Nouvelle Calédonie et dependences. ORSTM, Paris.
Phillips, A. & A. Lamb. 1996. Pitcher plants of Borneo. Kota Kinabalu: National History Publications.
SPSS, Inc. 2000. Systat for windows: statistic, ver. 10.0, Chicago, Illinois: SPSS, Inc.

Appendix

Specimens examined.

***Nepenthes vieillardii* Hook. f.:** Vieillard 1121 (P) Syntype, Deplanche (Vieillard 1121) (P) Syntype, Green 1816 (P), Pompery 505 (P), Stauffer 5738 (P), Virot 483 (P), Morat 8025 (P), McPherson 3380 (P), Lerat 1103 (P), Germain No number (P), Daniker 194 (P), Buchhols 1262 (P), Cribs 666 (P), Franc 17 (P).

***Nepenthes vieillardii* var. *deplanchei* Dubard;** Deplanche 211 (P) Syntype, Deplanche 100 (P) Syntype, Hurlimann 100 (P), Baumann 616 (P), Baumann 14,101 (P), Guillaumin & Baumann 9996 (P).

***Nepenthes vieillardii* var. *montrouzierii* Dubard;** Pancher No number (P) Type, Bernier 48 (P), Virot No number (P).

***Nepenthes vieillardii* var. *minima* Guill.;** Virot No number (P) Holotype.

Received July 21, 2003 ; accepted August 18, 2004